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Notes on the Cloacal Protuberance, Seminal Vesicles, and a Possible Copulatory Organ in Male Passerine Birds[1]

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Introduction

In a previous note we called attention to the cloacal protuberance as a means for determining breeding condition in some male passerines (Wolfson, 1952a) . We also described a method for obtaining motile sperm. The purpose of this paper is to report some of our observations on the protuberance and its related structures and to review the information that we have found in the literature. An examination of the notes below reveals the excellent opportunities for handers and collectors to discover important facts about the protuberance and the reproductive cycles in birds.

Although the protuberance has long been known to collectors and is an extremely conspicuous structure little is known about it. It was described for the first time apparently in a note by Fatio (1864) . Most surprising is that there is no mention of it in the recent, extensive experimental studies on the reproductive cycle in the slate-colored junco, Oregon junco, English sparrow, and starling (see Burger, 1949, and Wolfson, 1952b for reviews and bibliographies) .

[1]The research reported in this paper has been aided by a grant from the Graduate School of Northwestern University. Testosterone propionate (Perandren) was generously supplied by Ciba Pharmaceutical Products, Inc.

The only extensive study we know of which was directed specifically at gaining some understanding of the protuberance is that of Salt (1948) . Salt was particularly interested in the form and anatomy of the protuberance. His observations were made on specimens collected during spring migration and the breeding season in two successive years at Edmonton, Alberta. Two species were studied in detail, the horned lark *(Eremophila alpestris)* and the vesper sparrow *(Pooecetes gramineus)*. I am much indebted to Mr. Salt for his generosity and permission to report on his unpublished data. Our observations were made on captive birds at all seasons of the year over a period of seven years, and were incidental to our study of the gonadal and fat responses to day length. They include, however, continuous observation of individual birds, in many cases for longer than a year. As far as we know, the protuberance in captive birds under natural and experimental conditions of day length is identical to that which appears in wild individuals. A possible exception is that it may be slightly smaller in captive birds.

Witschi (1945) and Riddle (1927) have studied the reproductive ducts of male passerines and have contributed important data on the occurrence and size of the seminal vesicles and the factors which govern their development. The growth of the seminal vesicles is responsible for the appearance of the cloacal protuberance.

Notes on the Cloaca, Cloacal Protuberance, and Seminal Vesicles

Occurrence, by species. In our studies we have seen only passerine birds and most of these were fringillids. Salt has examined numerous passerines and a few individuals of non-passerine species, but only the godwit *(Limosa f edoa)* , lin gull *(Larus pipixcan),* mallard *(Anas platyrhynchos),* and sharp-tailed grouse *(Pediocetes phasianellus)* , among the non-passerines, were examined during the breeding season.

A variety of passerines exhibit a cloacal protuberance, but it has not been observed in any non-passerine species. The species in which it has been observed are listed in Table 1. There is some question about its occurrence in the English sparrow and starling despite the extensive studies on these species. However, there is no question about the seasonal growth of the seminal vesicles in these species. This matter is discussed further in the section below on form.

Occurrence, in time. All of the available observations point clearly to the existence of the protuberance only during the breeding season. We have not observed a fully developed protuberance in transient individuals, but its beginning is evident in some late migrants (May) . This is significant since the testes in many transients are already in "breeding condition" and show completely developed sperm. However, the seminal vesicles are enlarged. Possibly they contain some sperm. We have not made a histological study of the vesicles in transients.

Figure 1 portrays the reproductive organs in a slate-colored junco captured on April 25 and autopsied on May 4. Compare the size of the testes and seminal vesicles with the specimen in Figure 2 which was autopsied on June 8. In terms of length and width which are shown in the figures, the vesicles do not appear markedly different, but compare their weights and the relevant data which are given in Table 2. The marked increase in depth (dorsoventrally or anterioposteriorly depending on whether one thinks in terms of the body wall or the protuberance) is correlated with the marked increase in weight and is evidently responsible for the enlargement of the protuberance as the breeding season progresses.

External form. There are two and possibly three types of protuberances with respect to external form. Salt records a bulbous type only in the vesper sparrow and a tapering cylindrical type in the horned lark and other species. We have noted these two types, especially the bulbous type which seems to be characteristic of fringillids (Fig. 3) . In Table 1 the type of protuberance has been indicated where the author has described it, or where we have been able to determine it from the description.

The bulbous type is produced by the discrete nodular form of the seminal vesicles which appear conspicuously side by side in the posterior wall of the protuberance. They so distend the wall that the vent in ventral view appears to lie anteriorly, whereas normally it is centrally located (Fig. 3) . The bulbous form is due also to the small difference in the length and diameter of the vesicles. The cylindrical type of protuberance is longer and narrower, and, concomitantly, the seminal vesicles are narrow and shallow ellipsoids. Moreover, they are more lateral in position and do not meet on the midline in the posterior wall of the protuberance (Salt) .

Another possible type of protuberance is that seen by us in the English sparrow. However, we have examined too few specimens to be certain of its form. In this type the seminal

Table 1. Occurrence and Type of Cloacal Protuberance in Passerine Birds*

Family and Species	*Type*	*References*
ALAUDIDAE		
Horned Lark *(Eremophila alpestris)*	Cylindrical	Salt
MIMIDAE		
Catbird *(D u in etella carolinensis)*	Cylindrical (?)	Riddle
TURDIDAE		
Robin *(Turdus migratorius)*	Cylindrical	Mason, Riddle, Salt
PRUNELLIDAE		
Alpine Accentor *(Prunella collaris)*	Bulbous (?)	Fatio
PARULIDAE		
Palm Warbler *(Dendroica palmarum)*	(?)	Wolfson
Oven-bird *(Seiurus aurocapillus)*	Cylindrical (?)	Riddle, Wolfson
Yellow-throat *(Geothlypis trichas)*	(?)	Wolfson
American Redstart *(Setophaga ruticilla)*	Bulbous (?)	Mason
PLOCEIDAE		
English Sparrow *(Passer domesticus)*	(?)	Salt, Wolfson
ICTERIDAE		
Meadowlark *(Sturnella magna)*	Cylindrical	Salt
Red-wing *(Agelaius phoeniceus)*	Cylindrical	Salt
Brewer's Blackbird *(Euphagus cyanocephalus)*	Cylindrical	Salt
Cowbird *(Molothrus ater)*	Cylindrical (?)	Salt, Wolfson

*The citations for each reference are given in the list of the literature cited at the end of the paper. The type of protuberance has been determined in our studies and those of Salt. In other cases, it is based on the description of the author. One discrepancy is Salt's statement that he observed the bulbous protuberance in the vesper sparrow only, yet he saw a protuberance in many species of "sparrows." In our studies all of the fringillids clearly showed a bulbous type. Mason states that he found a bulbous protuberance in many fringillids. Perhaps in the individuals which Salt examined the protuberance was not fully developed.

Table 1, continued

Family and Species	*Type*	*References*
FRINGILLIDAE		
Indigo Bunting *(Passerina cyanea)*	Bulbous	Wolfson
Towhee *(Pipilo erythrophthalmus)*	Cylindrical (?)	Riddle, Wolfson
Spotted Towhee *(Pipilo maculatus)*	Cylindrical	Salt
Savannah Sparrow *(Passerculus sandwichensis)*	Bulbous (?)	Salt
Vesper Sparrow (Pooecetes *gramineus)*	Bulbous	Salt
Slate-colored Junco *(Junco hyemalis)*	Bulbous	Salt, Wolfson
Chipping Sparrow *(Spizella passerina)*	Bulbous	Wolfson
Field Sparrow *(Spizella pusilla)*	Bulbous	Wolfson
Harris's Sparrow *(Zonotrichia querula)*	Bulbous	Wolfson
White-crowned Sparrow *(Zonotrichia leucophrys)*	Bulbous	Wolfson
White-throated Sparrow *(Zonotrichia albicollis)*	Bulbous	Wolfson
Fox Sparrow *(Passerella iliaca)*	Bulbous	Wolfson
Lincoln's Sparrow *(Melospiza lincolnii)*	Bulbous	Wolfson
Swamp Sparrow *(Melospiza georgiana)*	Bulbous	Wolfson
Song Sparrow *(Melospiza melodia)*	Bulbous	Wolfson
McCown's Longspur *(Rhynchophanes mccownii)*	Cylindrical	Salt
Chestnut-collared Longspur *(Calcarius ornatus)*	Cylindrical	Salt
Canary (Domesticated)	Cylindrical	Wolfson

vesicles enlarge markedly laterally, but are shallow and do not induce a marked distension of the cloacal region. Hence, the protuberance is low with the seminal vesicles located laterally at its base. There is no question of the marked increase in the size of the seminal vesicles or their diffuseness (Fig. 4) . We do not have any measurements of this protuberance,

probably owing to the fact that it did not seem greatly elevated from the body wall. Salt and Witschi indicate that a protuberance occurs in the English sparrow, but neither one describes it. Further studies of this species and the starling in nature are needed.

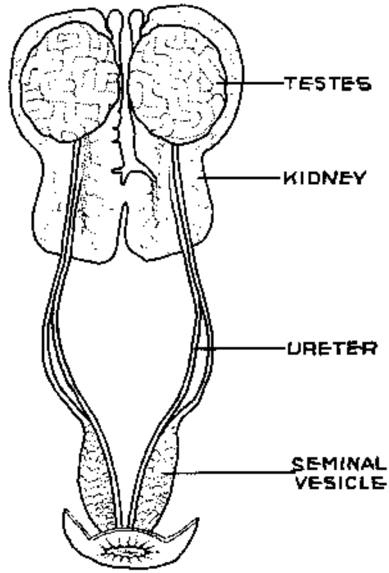

Figure 1. Diagram of the reproductive organs of a male slate-colored junco *(Junco hyemalis)* prior to occurrence of fully developed cloacal protuberance. Ventral view, diagrammatic. Enlarged about three times. Specimen (no. 335) autopsied May 4, 1951. This bird was held under natural day lengths since capture early in April. See Table 2 for measurements of seminal vesicles and testes.

It seems desirable to describe and measure the cloaca in breeding male passerines, a task which banders can well undertake. Other types of protuberances may turn up, and specific types may prove to be characteristic of different passerine families. In Table 3 measurements of the protuberance obtained in our studies are summarized. We have found only small differences in size in the fully developed protuberance of individuals in the same species, but variation may be

greater under natural conditions when breeding takes place. The largest measurements recorded in the literature are for the seminal vesicles of the accentor *(Prunella alpinus)* which were 12 mm. long and 8 mm. wide. Riddle states that the anal region projects backward "for almost a centimeter" in the

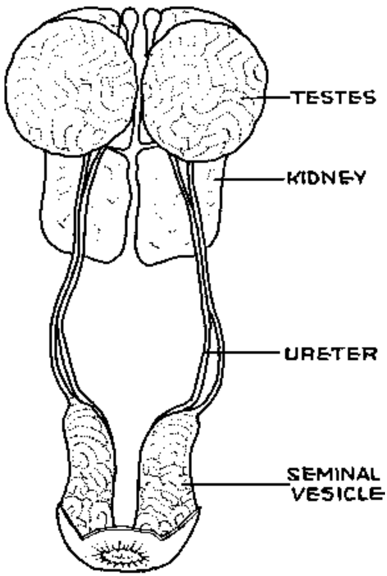

Figure 2. Diagram of the reproductive organs of a male slate-colored junco *(Junco hyemalis)* in breeding condition with fully developed cloacal protuberance. Ventral view, diagrammatic, with protuberance pulled posteriorly. Enlarged about three times. Specimen (no. 665) autopsied June 8, 1951. This bird was caught April 6, and was exposed to 20-hour day lengths until autopsied. See Table 2 for measurements of seminal vesicles and testes.

catbird, robin, and towhee. The largest protuberance that we have seen was in a white-throated sparrow which was exposed to continuous light soon after its capture early in May. On June 3 its protuberance was 7 mm. high and 10 mm. at its largest diameter. It was interesting to observe that the protuberance appeared almost equally large in species with markedly different body size and weight. In the fully developed protuberance of the vesper sparrow, Salt states that the greatest diameter is nearly 12 mm. If this is accurate for a

species of this size, then perhaps birds in nature achieve a greater development than we have seen in our captive birds even when they are exposed to highly stimulating day lengths or continuous light.

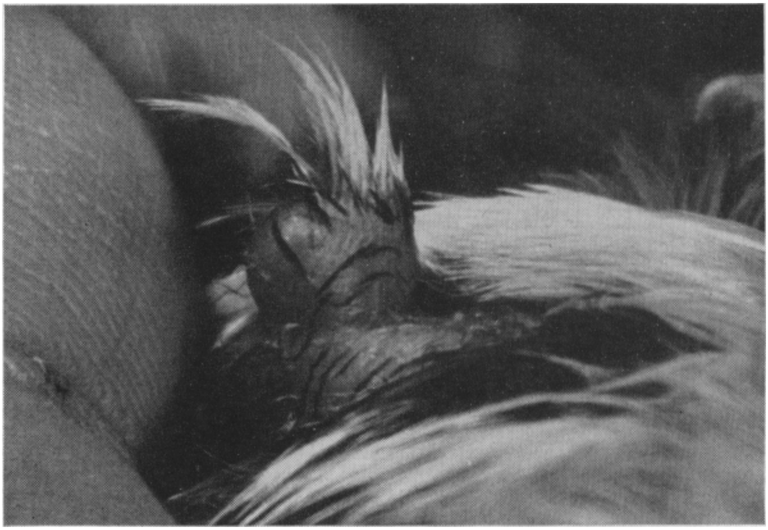

Figure 3. Cloacal protuberance in an adult male swamp sparrow (*Melospiza georgiana).* (Anterior is toward the right.) Note the outline of the nodules on the posterior wall and the relative displacement of the cloacal opening (not visible, but surrounded by anal tuft of feathers) toward the anterior wall of the cloaca. Normally, the opening is centrally located. Photographed on June 23, 1952, enlarged approximately five times. Reduced about two times. Actual measurements in the living bird were as follows: height of anterior wall 6.2 mm.; height of posterior wall 6.7 mm.; largest diameter (near top) 7.0 mm. This bird was caught the previous fall and held in captivity under natural conditions of day length.

Anatomy. The problem of the anatomy of the protuberance entails a consideration of the cloaca proper, the seminal vesicles and their related ducts, and the relation of these two fundamental parts to the pelvis, body wall, and other tissues which comprise the protuberance. The cloaca in passerine birds is a short, narrow canal which consists of three continuous but well defined chambers : the proctodeum, the uro-

deum, and the coprodeum. The proctodeum is the most distal of the three and its opening to the exterior is called the anus or vent. The urodeum follows next and receives the ureters from the kidneys and the vasa deferentia from the testes.

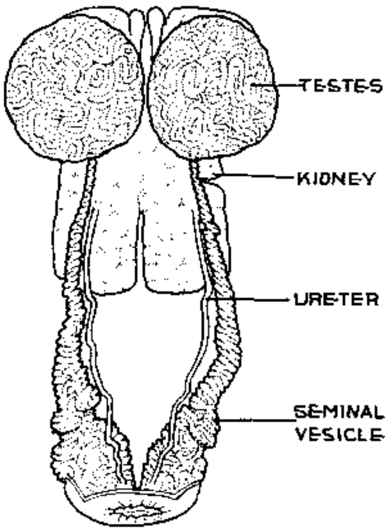

Figure 4. Diagram of the reproductive organs of a male English sparrow *(Passer domesticus)* after slight regression of reproductive activity. Ventral view, diagrammatic. Enlarged about three times. Specimen (no. 85) autopsied June 16, 1949. This bird was held under 8-hours of light per day from May 27 to June 16. Prior to May 27 it was exposed to natural day lengths. See Table 4 for measurements of seminal vesicles and testes.

The vasa deferentia empty through two conical papillae about 1 mm. in length. The most proximal chamber, the coprodeum, connects with the large intestine. These chambers are present in the non-breeding as well as the breeding condition. With the development of the seminal vesicles during the breeding season the cloaca takes on the appearance of a protuberance, but this is caused apparently by the growth of the seminal vesicles. The cloaca itself appears more vascular and its walls are thicker, but on the whole it does not appear to be greatly enlarged. A detailed study of the seasonal changes

Table 2. Data on Reproductive Organs of Specimens Illustrated in Figures 1 and 2*

Name and Number	*Date of Autopsy* (and Prior Treatment)	*Measurements of Testes* Length x Width - Volume	*Measurements of Seminal Vesicles* Length x Width x Depth - Weight
Slate-colored Junco #335 (Figure 1)	May 4, 1951 (Natural day lengths since capture, April 25)	L. 5.3 x 4.5 mm. - 56.2 $mm.^3$ R. 5.7 x 5.4 mm. - 87.0 $mm.^3$	L. 6.0 x 1.5 x .7 mm. - 2.8 mg. R. 6.0 x 1.5 x .7 mm. - 3.6 mg.
Slate-colored Junco #665 (Figure 2)	June 8, 1951 (20 hrs. light per day beginning April 6)	L. 6.8 x 5.2 mm. - 96.3 $mm.^3$ R. 6.2 x 5.8 mm. - 109.2 $mm.^3$	L. 8.0 x 3.5 x 5.5 mm. - 40.4 mg. R. 8.0 x 3.5 x 5.5 mm. - 43.2 mg.

*Length and width of testes were measured after preservation, with testes attached to body wall. Seminal vesicles were measured after preservation and dissection.

Table 3. Size of the Cloacal Protuberance in Some Male Passerines

Species	*Experimental Treatment*	*Date Measured*	*Measurements**
Towhee *(Pipilo erythrophthalmus)*	Natural day lengths since capture, Spring, 1951	July 3, 1951	3.5 X 3.5 X 9.0
Slate-colored Junco *(Junco hyemalis)*	20-hours of light per day since April 6, 1951	April 27, 1951	4.0 x 4.0 x 6.0
		May 18, 1951 (same bird as above)	6.5 x 7.0 x 6.5
		May 18, 1951	6.8 x 6.8 x 8.8
		May 18, 1951	6.8 x 6.8 x 6.8
		June 8, 1951	6.0 x 6.3 x 7.4
Field Sparrow *(Spizella pusilla)*	Natural day lengths since capture, April 7, 1951	June 9, 1951	4.0 x 5.0 x 6.0 (2 birds)
White-crowned Sparrow *(Zonotrichia leucophrys)*	20-hours of light per day from May 21 through May 31, then natural day lengths	June 3, 1951	6.1 x 9.8 x 9.7
White-throated Sparrow *(Zonotrichia albicollis)*	(a) Natural day lengths since capture, May 1951	June 3, 1951	5.0 x 5.0 x 8.0 (identical in 4 birds)
	(b) 24-hours of light per day since May 5, 1951	May 26, 1951	6.0 x 6.0 x 9.0 (identical in 2 birds)
		June 3, 1951	7.0 x 7.0 x 10.0
Swamp Sparrow *(Melospiza georgiana)*	Natural day lengths since capture, September 27, 1951	June 23, 1951	6.2 x 6.7 x 7.0
Song Sparrow *(Melospiza melodia)*	20-hours of light per day since April 6, 1951	May 4, 1951	5.0 x 6.0 x 6.5
		May 4, 1951	5.0 x 5.0 x 6.0
		May 10, 1951	5.0 x 4.6 x 6.4
		May 10, 1951	7.5 x 7.0 x 7.5

*Measurements are given in mm. in the following sequence: anterior wall, posterior wall, diameter. The *anterior wall* is measured from the body wall to the distal surface of the cloacal lips; the *posterior wall* is measured from the base of the visible nodules to the distal surface of the cloacal lips; the *diameter* is measured at both the base and distal part of the protuberance, from left to right and from anterior to posterior. Only the largest diameter is given here. It is usually the diameter at the base, but it may be the anterior-posterior diameter at the widest distal part where the nodules protude posteriorly. All measurements were taken with a dial caliper calibrated in tenths of a mm.

in the cloacal chambers remains to be made. The description which follows is based on the examination of the bulbous type of protuberance in preserved, freshly killed, and living individuals with the aid of a binocular dissecting microscope using a magnification of 10 times.

The most conspicuous feature of the protuberance is, of course, the large seminal vesicles which extend laterally and posteriorly, but not ventrally to the cloaca. Their connection with the cloaca is made through short thick ducts which leave their ventral (or anterior) face and enter the urodeum at the junction of its lateral and ventral walls. These ducts, known as the ejaculatory ducts, form conical papillae about 1 mm. high which lie close together against the ventral wall of the urodeum in preserved specimens. The ducts exit at the tips. Salt states that the papillae are projected obliquely forward (proximally) toward the coprodeum when the cloaca is in its normal position, but they project backward (distally) when the proctodeum is everted. We have seen the papillae directed only distally in both preserved and living specimens. The distal portions of the papillae appear red in live specimens after sperm have been obtained by the method described earlier (Wolfson, 1952a) . This is interpreted as indicating marked vascularity and possible cavernous nature and erectility of the papillae.

The urodeum connects distally with the proctodeum into which it empties its products. To fully appreciate the remarkable nature of the proctodeum one must examine it under the dissecting microscope in a live bird or in a freshly killed specimen. The preserved condition is not adequate. The characteristic feature of the proctodeum is the looseness of its lining which appears folded, especially so along its posterior (or dorsal) wall. It appears likely that it is cavernous since a conical papilla-like structure about 1.5 mm. long can be protruded from the vent. This papilla is formed by what appears to be the filling of two areas of the loose lining of the posterior wall of the proctodeum. Whatever the cause, the result is the elevation of two "sacs" which meet on the midline, are convex in their ventral aspect, and are sufficiently elongated to protrude from the vent. A definite, more or less covered groove is formed by their meeting on the midline and it exits at the tip of the papilla. Under the microscope one can readily "follow" the flow of fluid material in this groove. When

sperm smears are obtained under ideal conditions the exudate leaves the tip of the papilla and forms a pin-point of semen on the microscope slide. We have not observed the exact relation between the papillae of the vasa deferentia in the urodeum and the papilla formed by the wall of the proctodeum, but their location is such that it seems as though the papillae in the urodeum can pour their product directly into the groove formed in the papilla of the proctodeum.

The proctodeal papilla in these small passerines seems to me to be analogous to the copulatory organ which Burrows and Quinn have described in the rooster (1947) . In the rooster, Burrows and Quinn state that the papillae of the vasa deferentia lie directly over the groove of the erected organ. Moreover, they point out that the fully erected and exposed organ is like a semi-developed mammalian penis or over-developed clitoris in the female mammal.

Since the papilla in passerines is normally concealed within the proctodeum, its protrusion through the vent is caused either by its own erectility or the retraction of the wall of the proctodeum, or both. A small amount of pressure on the cloacal protuberance will cause its protrusion and occasionally it will remain protruded after the pressure is released. Its appearance and color suggest a highly vascular structure.

The final chamber of the cloaca, the coprodeum, connects with the large intestine. Its lining appears somewhat folded, but it did not appear to have any significant anatomical relation to the structures involved in reproduction. The fecal matter, of course, passes through the urodeum and proctodeum on its way to the exterior.

As was noted earlier, an understanding of the anatomy of the protuberance entails knowledge of the cloaca and the seminal vesicles and their relation to the body wall and related tissues. Having discussed the cloaca, there remains a consideration of the seminal vesicles and their relation to the cloaca and body wall. Some of the pertinent observations have already been considered in the description of the types of cloacal protuberances.

One of the fundamental problems relating to these extensive bodies in the protuberance is their nature and name. Bullough, in his extensive studies of the reproductive cycle of British and Continental starlings (1942) , states that the

vasa deferentia are closely coiled near the cloaca and give off numerous blind branches. He calls the compact bodies which are formed seminal vesicles. Witschi, who studied the starling in the United States (1945) , states that the vasa deferentia form "an entanglement of loops gathered into a pear-shaped body," and he calls this body the seminal glomus. Moreover, he states that "seminal vesicles are entirely lacking." Salt (1948) made a careful study of the relations of the tubules of the seminal vesicle and concluded that there were no branches of the vasa deferentia. Since the term glomus means a coil or small plexus, Salt prefers this term to vesicle, which means a small bladder. However, it must be borne in mind that the seminal vesicle in many mammals is a contorted, branched, saccular, glandular diverticulum of the vas deferens. Since the vesicle in birds is not actually a diverticulum of the vas deferens but a "coiling" of it, the term glomus might be more suitable. On the other hand, from a functional standpoint the vesicle in birds could be termed properly a seminal vesicle. This would not be as inaccurate as speaking of the distal part of the large intestine as the rectum in birds. Since the rectum originates in mammals from the subdivision of the cloaca, birds cannot have a rectum unless one uses the term in a functional sense to indicate the site of fecal accumulation before elimination. Riddle, in his discussion of their cyclical growth and regulation by hormones, refers to these enlargements of the sperm ducts as the vesiculae seminales. Going back to an earlier source, Coues (1884) states that specially formed seminal vesicles or seminal reservoirs are absent in birds, "though certain contortions and dilatations of the sperm ducts which are to be observed may imperfectly answer to detain the secretion until circumstances render it available." Disselhorst (1897) states that in most birds the vasa deferentia are dilated at their ends, and that these dilatations must be interpreted as non-glandular seminal receptacles.

Leaving the matter of terminology and possible differences in species for the future, it is clear that the vasa deferentia are responsible for the formation of the highly coiled, pear-shaped bodies which produce the protuberance in the cloacal region, and which, for the present, we shall call seminal vesicles. An understanding of their morphology entails knowledge of the gross and microscopic anatomy in their active, inactive, and transitional stages and their relation to

the cloaca and structures in the pelvis. Bullough (1942) has described the seasonal histological and gross changes in the seminal vesicles in the starling, but he does not relate them to the cloaca or a protuberance. Salt (1948) has made a detailed study of the histology and gross anatomy of the vesicles in the vesper sparrow and horned lark during the breeding season and describes their relation to the cloaca and the protuberance. Riddle (1927) and Witschi (1945) present data on the growth of the vesicles in relation to hormonal and other factors. Our observations are limited to a few weights and measurements and some observations on the relation of the vesicles to the pelvis and cloaca, some of which have been described above. The observations on the seasonal changes all agree on the extremely small size of the vesicle in the non-breeding condition and its large size in the breeding condition. In Table 4 some data on the vesicles and corresponding testes are summarized.

The microscopic structure of the "tubules" of the vesicles is similar to that of the vas deferens (Bullough, Salt) . The epithelial lining is cuboidal to columnar depending on its activity, and rests on a thin layer of connective tissue. This is surrounded by a circular layer of smooth muscle cells which is covered by a dense sheath of connective tissue. All of these layers show structural changes as the vesicles grow or regress. In the active seminal vesicle the epithelial lining appears to be highly secretory, and the lumen is about 20 to 30 times larger than in the inactive condition. Bullough states that the epithelium is ciliated. Salt describes ragged strands extending from the distal ends of the cells, but no cilia in the vesper sparrow. In the indigo bunting we observed a condition similar to that in the vesper sparrow.

In the inactive condition the seminal vesicle is retroperitoneal and lies against the muscles at the posterior border of the pelvis. As development proceeds the vesicle apparently grows distally from this point to form the bulbous type of protuberance. Most of the vesicle, therefore, lies outside of the abdominal cavity, but it is still covered with peritoneum. In the English sparrow and other species which do not have a bulbous protuberance much of the vesicle remains in the abdominal cavity and can be seen lying against the muscles of the pelvis. These differences in species are distinct and merit further careful study.

Table 4. Measurements of Seminal Vesicles and Corresponding Testes*

Species	Source	State	Date	Data on Seminal Vesicles and Testes: Vesicles		Testes	
Wood Thrush	Riddle	Active	June 5	L.	65.6 mg.	L.	378.7 mg.
(Hylocichla mustelina)				R.	75.8 mg.	R.	367.5 mg.
		Inactive	Sept. 7	L.	3.6 mg.	L.	3.9 mg.
				R.	3.0 mg.	R.	3.9 mg.
Robin	Riddle	Active	April 29	L.	301.4 mg.	L.	753.6 mg.
(Turdus migratorius)				R.	326.0 mg.	R.	840.0 mg.
		Inactive	Sept. 12	L.	4.7 mg.	L.	5.2 mg.
				R.	5.2 mg.	R.	5.3 mg.
		Inactive	Sept. 12	L.	2.5 mg.	L.	3.0 mg.
				R.	2.2 mg.	R.	3.0 mg.
Ovenbird	Riddle	Active	May 13	L.	21.3 mg.	L.	.7 mg.
(Seiurus aurocapillus)				R.	50.5 mg.	R.	405.5 mg.
		Active	May 28	L.	59.0 mg.	L.	243.8 mg.
				R.	67.5 mg.	R.	290.8 mg.
		Active	June 4	L.	58.2 mg.	L.	178.4 mg.
				R.	70.2 mg.	R.	204.0 mg.
		Active	June 26	L.	64.5 mg.	L.	250.0 mg.
				R.	63.5 mg.	R.	181.8 mg.
Starling	Witschi	Active	Mar. 8	L.	6.0 mg.	L.	40.0 mg.
(Sturnus vulgaris)				R.	6.2 mg.	R.	47.0 mg.
		Active	Mar. 24	L.	13.0 mg.	L.	204.0 mg.
				R.	12.0 mg.	R.	201.0 mg.
		Active	Mar. 24	L.	15.0 mg.	L.	428.0 mg.
				R.	17.0 mg.	R.	440.0 mg.
		Active	April 13	L.	168.0 mg.	L.	966.0 mg.
				R.	190.0 mg.	R.	989.0 mg.
		Active	April 22	L.	143.0 mg.	L.	661.0 mg.
				R.	133.0 mg.	R.	615.0 mg.
		Inactive	Nov. 4	L.	3.0 mg.	L.	3.3 mg.
				R.	2.8 mg.	R.	3.0 mg.

English Sparrow	Wolfson	Active	April 6	L. 6.0 mg.	L. 131.5 mm.^{3}
(Passer domesticus)				(2.5 x 2.0 X 2.0)[1]	
				R. 5.0 mg.	R. 129.4 mm.^{3}
				(3.0 x 2.5 x 1.9)	
		Active	June 16[2]	L. 24.8 mg.	L. 171.4 mm.^{3}
				(6.0 x 4.0 x 3.0)	
				R. 25.8 mg.	R. 179.6 mm.^{3}
				(7.0 x 4.8 x 3.7)	
Indigo Bunting	Wolfson	Active	June 6	L. 41.0 mg.	L. 192.5 mm.^{3}
(Passerina cyanea)				(7.0 X 3.5 X 5.5)	
				R. 35.8 mg.	R. 131.9 mm.^{3}
				(7.0 x 3.6 x 5.0)	
White-throated Sparrow	Wolfson	Active	June 4	L. 50.4 mg.	L. 306.7 mm.^{3}
(Zonotrichia albicollis)				(7.5 x 5.0 x 4.0)	
				R. 49.4 mg.	R. 495.9 mm.^{3}
				(7.5 x 5.5 x 4.0)	
		Active	June 4	L. 37.6 mg.	L. 225.5 mm.^{3}
				(6.7 x 4.0 x 4.9)	
				R. 21.6 mg.[3]	R. 138.3 mm.^{3}
				(6.5 x 4.0 x 4.9)	

*In Witschi's and Wolfson's studies the weights of the seminal vesicles are wet weights after preservation and include the part of vasa deferentia which extends from the posterior edge of the metanephros to the seminal vesicle. In Riddle's study only the seminal vesicle was weighed but no statement is made regarding condition at the time of weighing. Specimens of Riddle and Witschi were collected in nature. One specimen of Wolfson which was exposed to experimental day lengths is indicated.

[1]These figures represent the length, width, and depth of the seminal vesicles (see Table 2).

[2]The seminal vesicles, vasa deferentia, and testes are illustrated in Figure 4. On June 16 showed signs of regression. This bird was exposed to 8 hours of light per day from May 27 to June 16.

[3]The right testis showed signs of regression which is reflected in the smaller weight of the right seminal vesicle.

A final feature in the bulbous type of protuberance which also merits further study is a thin band of tissue which lies against the dorsal face of the vesicle at about its middle, and extends from the ventral surface of the pelvis to the cloacal wall. It may be supportive, or it may function in compressing the vesicle and hence aid in ejaculation.

Function. In considering function one must differentiate between the function of the parts and how they function. Moreover, one must keep in mind that the determination of function in this instance rests entirely on interpretation. No experimental work has been performed.

There is complete agreement on the storage of sperm in the seminal vesicles and portions of the vasa deferentia. There is also some agreement that the appearance of the epithelium of the vesicle is indicative of secretion. The seminal vesicles, therefore, possibly provide a medium for the transport and nourishment of the sperm. Further extensive studies are needed. Another possible function is to provide a place for the maturation of the sperm, as occurs in the epididymis of mammals. In his studies of fowl sperm, Munro (1938) demonstrated functional changes in the sperm as they passed through the excurrent ducts of the male. The sperm attained a functional maturity during their passage through the epididymis and /or the first part of the vas deferens. This maturation, which is manifested by their ability to show movement and enables them to accomplish fertilization, rarely occurs in the testis or epididymis. We attempted to determine the motility of sperm in the testis and ducts of a few male passerines which had fully developed protuberances. Motile sperm were obtained in good numbers consistently from the seminal vesicles, but were never obtained from the testis. The tests of the epididymis and vas deferens were unsatisfactory. The seminal vesicles would be an excellent place for the maturation and storage of sperm, especially so since in the bulbous protuberance their temperature is several degrees cooler than the body temperature (Wolfson, unpublished data) .

Another possible function of the protuberance is to assist in coition. With the elevation of the cloaca from the body wall and the extrusion of the conical papilla from the proctodeum better contact with the cloaca of the female is possible. It also seems possible that during coitus the proctodeum of the female not only comes into contact with that of the male, but

"covers" the protuberance of the male, hence insuring the entrance of the semen into the opening of the oviduct. It is also possible that the papilla of the male is inserted into the opening of the oviduct. In the female there is no protuberance as in the male, but the cloaca is much enlarged during the breeding season, especially the proctodeum, and its thickened outer "lips" are easily distended and retracted exposing the urodeum and the opening of the oviduct in its wall. In the fowl, Burrows and Quinn (1937) state that the copulatory organ of the male enters the protruded oviduct of the hen.

Regulation of Development. Since the seminal vesicles are fully developed only during the breeding season one might think that their enlargement was caused by the flow of sperm into them. From the condition of the vesicles in two cases where a testis on one side failed to produce sperm, Riddle (1927) demonstrated that the growth of the vesicles is hormonally controlled. Witschi, who has made a more detailed study of the deferent ducts (1945) , concluded that three factors are responsible for their increase in weight during the breeding season : (a) hormone stimulated growth of walls ; (b) accumulation of spermatic fluid ; (c) growth, stimulated by functional stress of the epithelium of the ducts. In our laboratory we have found that the injection of male sex hormone (testosterone propionate) stimulates the growth of the seminal vesicles during the winter, but a fully developed protuberance could not be induced (unpublished data) . Our results, therefore, support Witschi's conclusions that both hormonal and mechanical factors are necessary for the complete development of the seminal vesicles.

Where observations have been made on the growth of the vesicles in relation to the growth of the gonad (Bullough, Salt, Wolfson) it is clear that the seminal vesicles begin their growth before the testes are fully developed. In fact, recrudescence of both organs occurs at about the same time, but the vesicles grow most rapidly and achieve full development only after the testes have reached breeding condition and remain in breeding condition for some time. Thus, in many species we have observed testes with sperm, but the protuberance was only slightly developed and the seminal vesicles were much smaller than their maximum condition (see Tables 2 and 4 and Figures 1 and 2) . A few data that we have

indicate that it takes from two to four weeks for the protuberance to reach its maximum size once it has begun to develop. Regression of the seminal vesicles and the protuberance is correlated usually with regression of the testes. In our experimental studies where we followed the breeding condition of numerous birds by means of sperm smears this correlation was clearly demonstrated. These observations on the relation between the gonadal cycle and the growth cycle of the seminal vesicles can also be interpreted as supporting Witschi's conclusions.

Significance of Seminal Vesicles and Protuberance in Laboratory and Field Studies

In laboratory and field studies it is frequently valuable to be able to determine the breeding condition of individuals without killing them. This can be done by means of the cloacal protuberance in many male passerines, by means of the seminal vesicles, or by the presence of motile sperm (Wolf son, 1952a) . The protuberance can also be used to sex individuals in species without sexual dimorphism (Mason, 1938, McCabe, 1943) . This would, of course, be restricted to the breeding season, but we have found that even in the non-breeding season the cloaca of the male, in juncos for example, differs from that in the female in having slightly elevated anterior and lateral walls. To put it another way, there is a slight angle formed by the ventral body wall and the anterior wall or lip of the cloaca in the male, whereas in the female the anterior wall or lip of the cloaca seems to pass almost imperceptibly into the body wall. This difference is reflected also in the place of origin of the feathers of the anal tuft. Through the use of this criterion and the length of the wing we have been able to sex correctly, as determined by autopsy later, over 95 per cent of the juncos we have trapped.

In using the protuberance as an indicator of breeding condition one must remember that although its presence (or occurrence of motile sperm) is an excellent indicator of breeding condition, its absence does not always mean that the testes are not undergoing spermatogenesis. In our experimental work we have found it necessary to autopsy birds when experimental conditions stimulated spermatogenesis yet precluded the formation of the protuberance. This raises a question and emphasizes an important point. In previous ex-

perimental work on the role of day length in the regulation of breeding cycles, the formation of spermatozoa in the testis has been regarded as the "breeding condition." But in view of the seasonal development of the seminal vesicles and the cloacal protuberance, should we not define specifically the extent of development in the testes *and seminal vesicle* and possibly reserve the term "breeding condition" for those individuals that show a fully developed cloacal protuberance ? We do not know, of course, if successful coition is dependent on a fully developed protuberance. Extensive field work will be needed to determine this. But until we know what " breeding condition" is, in terms of the accessory reproductive organs, it would be well to define precisely the reproductive condition achieved in experimental work and to exercise more caution in relating the results of experimental studies to conditions in nature.

A similar problem exists in defining the breeding season of populations in nature. They are usually defined by the occurrence of freshly laid or incubated eggs. Obviously this does not tell us anything about the gonadal cycle in the male, though it is often assumed that the period of activity in the male corresponds with that of the female. Where the gonadal cycle in the male has been studied by the collection of specimens and histological study of the testes (for example, Moreau, Wilk, Rowan, 1947) , the occurrence of free sperms in the testes coincided well with the *egg* laying period, but the size of the testes was not a valid indicator of stage of spermatogenesis. In most field studies, however, the collector only records the size of the testes on the assumption that the size alone is an indicator of breeding condition. In most cases this may prove to be true, but if the size of the testes *and* the condition of the seminal vesicles are recorded, one would have a much more accurate measure of reproductive condition. This is especially true for birds in the tropics where the difference in size between testes producing sperm and those that are not is considerably less than in temperate species. Moreover, even when a bird is collected with testes of maximum size, it might still be several weeks away from breeding. Bates (1927) in his studies of the birds of the Cameroon and Lake Chad region recognized the importance of fully developed seminal vesicles in determining breeding condition in males and cautioned that "large testes alone are

not very reliable evidence of breeding just at the time ; they may continue long after breeding is past." Chapin (1932) in his study of the birds of the Belgian Congo also comments on the importance of the "convoluted condition of the vasa deferentia which marks the peak of reproductive activity in the male." He comments further "that the size of the testes is a fair indicator of the season for breeding." For collectors who wish to record the condition of the vesicles some care must be exercised in the preparation of the skin to avoid cutting through them. Before the skin is prepared the occurrence and measurments of the protuberance, if any, may be noted. After the skin is prepared the vesicles can be exposed, measured, and the condition of the testes and vasa deferentia noted.

Using the criteria of cloacal protuberance and presence of motile sperm the maintenance of reproductive activity for over one year was demonstrated in a group of captive juncos subjected to experimental treatment (Wolfson, 1952b) . These criteria should also prove useful in studies where birds are trapped or banded.

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